

DISJUNCT SYNCHRONIC POPULATIONS OF 17-YEAR
PERIODICAL CICADAS: RELICTS OR
EVIDENCE OF POLYPHYLY?

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Abstract.—The theory and biogeography of brood formation in periodical cicadas is reviewed in light of the extraordinary number of different “broods” represented on Long Island and its immediate vicinity. Detailed emergence records, with dates and exact localities, are given in an appendix. We present data which suggest that the evolution of Brood I on Long Island may have been independent of the evolution of Brood I in Virginia. Possible evolutionary scenarios are discussed in light of allozymic and morphometric findings.

Periodical cicadas (Homoptera: Cicadidae: *Magicicada*) are confined to the eastern deciduous forest of the United States; they are not found in the largely coniferous forests of Canada and the northern United States (Marlatt 1907; Dybas and Lloyd 1974). During the most recent (Wisconsin) glacial advance, ending about 12,000 years ago, most of the periodical cicadas' present range was covered by spruce forests (Delcourt and Delcourt 1981 and references therein). It is doubtful whether the recent ancestors of *Magicicada* spp. could have lived in such forests. The species of trees now characteristic of the eastern deciduous forest were confined to small refugia along river courses in the southern United States. A dry oak/hickory/southern pine forest covered the southern states outside of the refugia except for peninsular Florida (sand dune scrub) and the Mississippi basin (cypress/gum).

Today, we find the three morphologically distinct species of periodical cicadas split up into 12 major dyssynchronous 17-year broods (*M. septendecim*, *M. cassini*, *M. septendecula*) and three 13-year broods (*M. tredecim*, *M. tredecassini*, *M. tredecula*), each with its characteristic range. These broods, or year classes, were mapped by Marlatt (1907). (Updated maps can be found in Lloyd and Dybas 1966; Dybas and Lloyd 1974; and Simon 1979a.) It is difficult to believe that the broods, as we know them today, could have existed prior to the Wisconsin glaciation. Periodical cicadas undoubtedly moved south with the deciduous forest as the ice advanced and must have

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migrated back north as the various tree species recolonized (Davis 1976). It is likely that the past 12,000 years have seen the active proliferation of new broods from one or a few ancestral broods. The most interesting feature of periodical cicada evolution is that whatever happened must have involved all three species because all can now be found coexisting in almost every brood.

Recently, it has become possible to bring new information to bear on the questions surrounding periodical cicada evolution, namely electrophoretic data on allozymes (Simon 1979a, b) and morphometric data on wing venation (Simon 1982). Thus the alternative evolutionary schemes, which flow rather easily from biogeography can now graduate from being idle speculation to being testable hypotheses.

We propose to treat this subject in full detail in a series of forthcoming papers, but our present purpose is more limited and sharply focused. Here, we will be immediately concerned with only five of the 17-year broods: XIV, X, IX, V, and I. All five of these broods co-occur on Long Island, New York. They must either have recently immigrated (since Long Island is a terminal moraine) or very recently have evolved in situ. It is rare to have so many different broods reported from so small an area. Most of our knowledge comes from the observations of one man, William T. Davis, who lived on Staten Island, New York for many years and kept a close watch for periodical cicadas emerging on Staten Island (Simon 1979c) and on Long Island (see Appendix I). According to these records, Long Island appears to be either (1) a microcosm of rampant evolution of cicada broods or (2) an area into which many broods have recently immigrated, with still more recent extinctions in large mainland areas, leaving behind relict populations of several broods.

In this paper, we bring together the available evidence from published records and unpublished correspondence concerning exact localities and emergence dates for the six periodical cicada broods known for Long Island. Each of these is compared biogeographically with the nearest known representative of the same brood on the mainland (i.e., those populations with adults emerging in the same year). As we discuss in detail below, all the Long Island "broods" except XIV, and possibly X, are disjunct, suggesting either a relict status or a polyphyletic origin, as described earlier (hence the quotation marks around broods). Further, we have collected adult specimens of Broods I and XIV from Long Island and from a representative sample of their geographic ranges and analyzed them phylogenetically using comparative wing-morphometric and allozymic data to test the theories of brood formation.

Although Long Island is an excellent place to study periodical cicadas, we should acknowledge the possibility that there may, after all, be nothing more unique about Long Island than the fact that William T. Davis was watching

it. Perhaps equally close observations on other areas would turn up many more cases of disjunct, relatively small, unrecorded populations which correspond to the emergence years of existing broods.

Theory of Brood Formation

A series of papers (Marlatt 1907; Alexander and Moore 1962; Lloyd and Dybas 1966; Lloyd and White 1976; White and Lloyd 1975, 1979; Simon 1979a, b, 1982; Simon et al. 1981; Lloyd et al. in prep.) has given us a theory of brood formation that postulates two kinds of accelerations in the cicadas' life cycle: (1) those of one year, supposedly brought about by a single historical episode of extraordinary weather, which affects an entire population within part of the range, and (2) those of four years, supposedly brought on by nymphal crowding which affects only part of a population and generates two broods four years out of phase which coexist in the same woodland.

Seventeen-year cicada broods.—If we take the centrally-located Brood XIV as the putative ancestral brood, then the formal scheme shown in Fig. 1 can be visualized. With both 1-year and 4-year accelerations occurring, it is possible to derive a given brood in two different ways (or more, if the scheme is extended). For example, Fig. 1 shows that Brood IX could be derived from X by a 1-year acceleration, or from XIII by a 4-year acceleration. The most immediate check we have on the validity of such hypotheses is biogeography. Thus the conversion $X \rightarrow IX$ (shown by a solid line in Fig. 1) was a likely event because Broods IX and X have broadly contiguous ranges in the Appalachians. Brood XIII, by contrast, is confined to northern Illinois and eastern Iowa, a less plausible derivation (therefore shown as a dashed line). In some cases, the biogeography is equivocal, e.g., $VI \rightarrow V$ and $IX \rightarrow V$ both involve broods with closely associated ranges, so each is represented by a solid line.

Broods III and IV pose a problem: they have nearly contiguous ranges through east central Kansas, Missouri and Iowa so we can reasonably derive III from IV, but none of the supposed ancestral broods—V (Ohio), VIII (Pennsylvania), VII (New York)—have ranges anywhere near those of III and IV. In this case, we would postulate that Brood IV came from a separate glacial refugium and III was subsequently derived from it. A less plausible alternative is that Brood V once existed in the Mid-West (where it was derived from VI, which is recorded from Wisconsin) but has since become extinct.

Thirteen-year cicada broods.—Lloyd and Dybas (1966) proposed that 4-year accelerations, by occurring repeatedly, might have been selected for and the process thereby become genetically assimilated (Waddington 1953, 1956). This scheme has the great advantage that it provides a mechanism whereby the 13-year life cycle can be derived from the 17-year one without

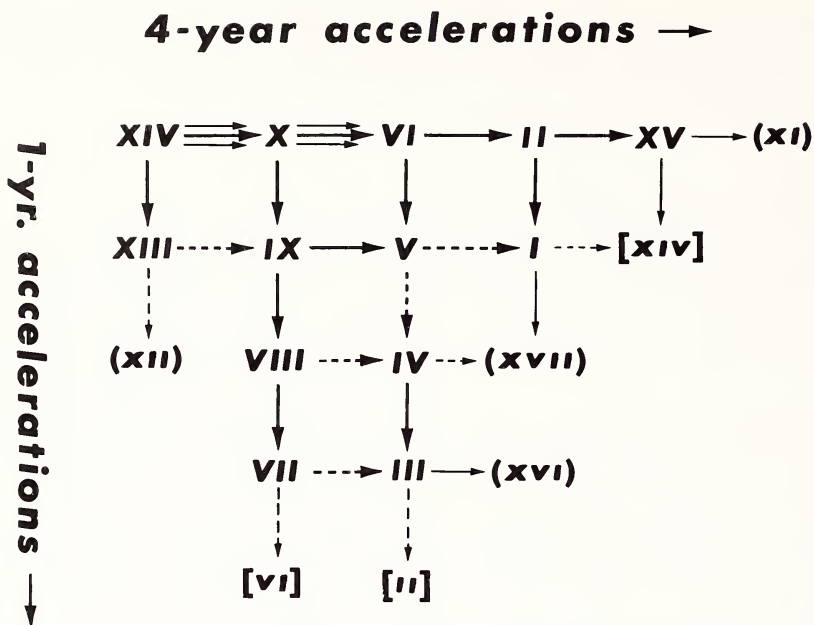


Fig. 1. Formal scheme for deriving all 17-year periodical cicada broods from the postulated ancestor, Brood XIV, by a combination of 4-year and 1-year accelerations, modified from Lloyd and Dybas (1966). Solid single arrows indicate that the two broods have contiguous or closely associated geographic ranges; dashed arrows, that they do not. Triple arrows indicate that the broods' ranges are closely associated in three different parts of the country, suggesting the possibility of polyphyletic origins. Broods in parentheses are of doubtful existence, consisting of very few records; no arrows lead from them. Broods in square brackets could be derived as shown, but there is no need to postulate such a derivation, since a simpler way exists to derive them, starting with Brood XIV.

losing the periodicity in the process (by the generation of intermediates) or the complete elimination of one life cycle by the other. The problem is that the biogeography does not seem to fit. The progression XIV → X → VI → II → XV → XI does make geological sense, but it ends up with the very small Brood XI in New England (Brood XI was well known to the Pilgrims but is now extinct; Lloyd and White 1976) while 13-year cicadas occupy a very broad range in the southern and Mississippi Valley states.

Biogeography might have us postulate that the 13-year cicadas existed in northern deciduous forest refugia during Wisconsin times. They may indeed have evolved from a progression of 4-year accelerations, like we now postulate for XIV → X → VI → II → XV → XI, but this may have happened during a previous interglacial period. This would not be a surprising conclusion, since there have been 16 interglacial epochs in the past two million years (Wright 1976), but we might still need to postulate a separate full-

glacial refuge for the 13-year cicadas. The alternative prediction would have 13-year cicadas evolving in the present interglacial, in situ in part or the whole of their present range by many 4-year accelerations from one or more 17-year parental broods. Allozymic data (Simon 1979a) suggest that the three or four 13-year broods which are not extinct evolved from a single 17-year ancestor. We may never know the history of the other 13-year broods which were last recorded in the early 1900's and late 1800's and were poorly collected.

The pattern of distribution of 13-year Brood XIX in relation to 17-year Broods III and IV suggests that 13-year cicadas may be advancing into the range of 17-year cicadas. Lloyd, Kritsky and Simon (in review) propose that hybridization between 13- and 17-year cicadas in zones of contact has led to the exclusion of the 17-year parental brood via nymphal competition from a second generation 13-year hybrid brood. They present the following genetic hypothesis: Parental generation—DD = 17-year and dd = 13-year; F1 generation—Dd = all 17-year; F2 generation—DD, Dd = 17-year and dd = 13-year, which could never breed with their 13-year grandparent's descendants, and could only breed with their 17-year sib's descendants every 221 years, but by that time the 17-year brood will have been eliminated from the area by nymphal competition.

Evidence for four-year accelerations.—The fact that the largest broods of 17-year cicadas overlap widely and are separated by four years suggested to Lloyd and Dybas (1966) that they could have been derived from each other by a 4-year shortening of the life cycle. They suggested that this shortening could occur through the temporary deletion of a postulated supernumerary 6th nymphal instar. White and Lloyd (1975) excavated 13- and 17-year cicada nymphs of the same age and found that rather than possessing an extra instar, the 17-year nymphs differed from the 13-year ones in that the 17-year nymphs grew much more slowly during the first four years of life. Lloyd and White (1976) postulated that this 4-year inhibition in growth might be broken by the stimulus of early nymphal crowding, leading part of the population to emerge four years ahead of schedule. Simon's (1979a) phylogenetic analysis of allozymic data for two 17-year broods and three 13-year broods is compatible with this scheme.

Three years after Lloyd and Dybas (1966) published their hypothesis, a 4-year acceleration was observed in the suburbs of Chicago, where literally hundreds of thousands of periodical cicadas emerged four years ahead of schedule. Only one brood of periodical cicadas (Brood XIII) had ever been recorded from that area, so these cicadas could have had no other origin. The remainder of the brood emerged, on schedule, in 1973, in enormous abundance (many millions) with negligibly few appearing during the intervening years. The two species present in Chicago, *Magicicada septendecim* and *M. cassini*, both participated in this event, although the many thousands

that emerged in 1969 were not enough to satiate predators, and apparently left negligibly few descendants (Lloyd and Dybas in prep.). If they had successfully reproduced, a disjunct population of Brood IX would have been created, living sympatrically with Brood XIII in Chicago.

Lloyd and White (1976) found Broods X and XIV living sympatrically in northern Kentucky and documented quantitatively the proportion of cicadas in each brood by measuring 4-year-old eggnest scars, and those of the current year (1974) after Brood XIV had emerged. They made the important theoretical point that once accelerated individuals establish a "beachhead" that is large enough to satiate predators, then conversion to the accelerated brood (Brood X in this case) can be a gradual process extending over many generations. There is a geographical gradient from mostly Brood XIV in Tennessee to mostly Brood X in Indiana, suggesting that the conversion is taking place at a faster pace farther north.

An interesting case exists in New Jersey where Brood XV, a very small brood, is located in counties noted for their abundance of Brood II. A few thousand individuals of Brood XV emerged in Union, Essex, and Bergen counties in 1975. This brood was recorded in these localities in the latter half of the 19th century (Weiss 1916), but no notice had been taken of them since that time. The cicadas that did emerge disappeared after only a week. It is unlikely that they left enough progeny to survive 17 years, emerge, and reproduce. Brood XV is probably not (and probably never has been) a self-reproducing brood, but rather has been regenerated each 17 years from particularly dense populations of Brood II. Observations of Brood II in 1979 proved that they appeared in abundance in *exactly* the same suburban yards where Brood XV had appeared in 1975 (C. Simon unpubl. field notes). In other words, Brood II may be in a very early stage of the process of converting to Brood XV, where there is as yet no "beachhead" of XV established.

A similar situation may exist with Brood VI. It is a very wide-ranging but strongly patchy brood found throughout the eastern United States (Marlatt 1907). Its modern range is poorly documented because of its patchiness. Brood VI is largely sympatric with Brood X, the next most wide-ranging of all the periodical cicada broods. If Brood VI was merely repeated 4-year accelerations of dense populations of X, then the scatter of VI-populations would be understandable. However, there are some counties in Georgia and North Carolina where populations of VI are reported, but none of X (Marlatt 1907). The conversion $X \rightarrow VI$ may therefore be in a stage intermediate between $XIV \rightarrow X$ and $II \rightarrow XV$, which is the progression one would expect if the ancestral brood were XIV (Figs. 1, 2).

Evidence for one-year accelerations.—Several examples can be found of broods that abut each other and are separated by one year (I–II, III–IV, VIII–IX, IX–X, XXII–XXIII). Broods separated by one year never overlap. Broods XXII and XXIII are known to occur less than one mile apart near

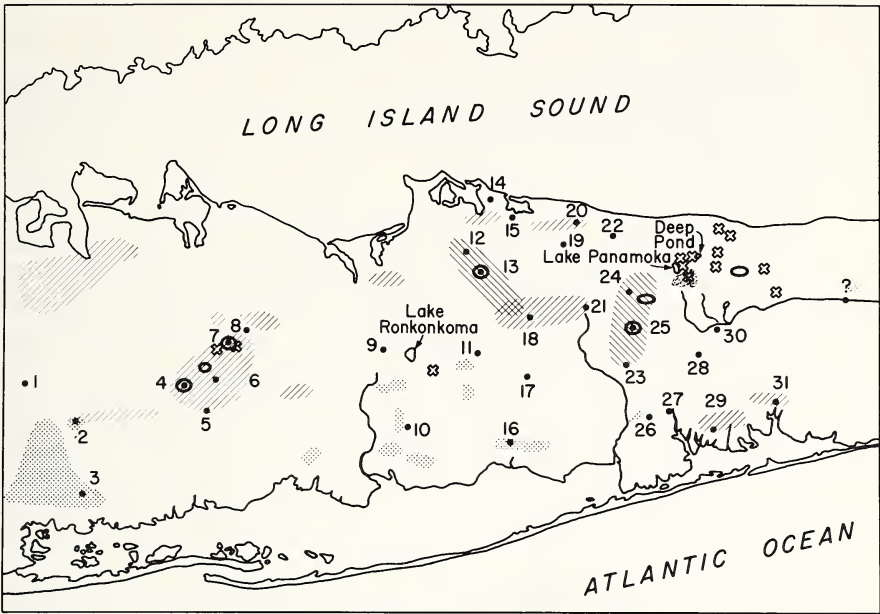


Fig. 2. Central Long Island, encompassing all periodical cicada records except possible Brood II, 1911 localities from Brooklyn (only a few individuals). Locality information is taken from W. T. Davis's field notes and publications, from newspapers, and from personal observations. These sources are detailed in Appendix I. The numbered dots are towns reporting Brood XIV (dates are given in Appendix I): 1 = Hicksville, 2 = Farmingdale, 3 = Massapequa, 4 = Wyandanch, 5 = Deer Park, 6 = Half-Hollow Hills, 7 = Dix Hills, 8 = S. Commack, 9 = Ronkonkoma, 10 = Bohemia, 11 = Farmingville, 12 = East Setauket, 13 = Port Jefferson, 14 = Belle Terre, 15 = Mount Sinai, 16 = Patchogue, 17 = Medford, 18 = Coram, 19 = Miller Place, 20 = Sound Beach, 21 = Middle Island, 22 = Rocky Point, 23 = Yaphank, 24 = Ridge, 25 = Brookhaven National Laboratories, 26 = Shirley, 27 = Mastic, 28 = Manorville, 29 = Center Moriches, 30 = Calverton, 31 = Eastport, ? = Riverhead. Crosshatching = Brood XIV from Davis's personal records. Inverse cross-hatching (upper left to lower right) = personal observations of C. Simon in 1974. Broods other than XIV are indicated as follows: light, regular stipple = Brood X; small, heavy circles or ellipses and hollow "x's" = Brood V; irregular stipple (near Lake Panamoka) = Brood IX.

Utica, Mississippi, as do Broods I and II in the George Washington National Forest near Luray, Virginia (C. Simon unpubl. field notes). Broods IX and X come close to overlapping, being reported from many of the same counties in West Virginia (Marlatt 1907), but there are no known cases of their occurring sympatrically in the same woods. (We predict that none will be found, for reasons given below.)

The usual geographic pattern is for the accelerated periodical cicada brood to replace its fellow farther to the north. Alexander and Moore (1962) suggested that, "... prolonged or repeated periods of extreme cold caused sum-

mation of diapauses . . . and thus caused those populations closer to the glacial boundary to emerge earlier." We now understand from more recent palynological studies (Delcourt and Delcourt 1981) that the deciduous forest refugia were nowhere near the glacial boundary, but the principle remains the same: a single historical episode of unusually cold weather could affect nymphal development.

The physiological machinery by which periodical cicadas seem to "count" 17 (or 13) years is still a mystery, but it could well be cued to some hormonal change taking place in their host trees. If unusual weather on some historical occasion could cause, say, unseasonal defoliation with a second leafing out later in the summer, the concomitant hormonal change in the tree might cause the cicada to "count" an extra winter and emerge one year ahead of schedule (Lloyd and White 1976). The important point is that one would expect all of the cicadas to be affected by such a change, not just a part of the population. For this reason, broods which are separated by one year would not be expected to overlap except by secondary movements which are known to occur slowly, if at all (Karban 1981; Lloyd, White, and Stanton 1982).

Theoretically, there are three reasons why broods one year out of phase should never coexist sympatrically in the same woods: (1) The climatic aberration by which they supposedly arose would be expected to affect the entire population, as just stated. This reasoning does not apply to 4-year accelerations if these arise through effects of crowding, which could well affect only part of a patchily-distributed population. (2) The numerical response of predators (Murdoch and Oaten 1975) should fall heavily on any brood lagging one year behind another, probably eliminating the lagging brood. Escape from predator build-up is theorized to be the whole advantage of coupling periodicity with the long life cycle. It enables periodical cicadas to satiate predators on every emergence, and presumably accounts for their great abundance compared with non-periodical cicada species (Lloyd and Dybas 1966). Parasitoids such as the tiny wasp *Lathromeris cicadae*, for example, prey heavily on periodical cicada eggs during an emergence year (Marlatt 1907), but must have alternative hosts in other years. After four years, the numerical response would surely have dissipated itself, so a brood lagging by four years should not be eliminated by this cause. (3) Newly-hatched nymphs of the leading brood will settle underground and have the advantage of being already established by the time young nymphs of the lagging brood appear. Given that the cicadas are very abundant, the leading brood may preempt all the suitable feeding sites, leaving nothing for the lagging brood. This and predator satiation are the two basic assumptions used by the model of Hoppenstaedt and Keller (1976) to explain the origin of periodicity. Their model works well, but depends sensitively on the suitable choice of parameter values (May 1979).

White and Lloyd (1979) report a case in northern Kentucky where sub-

stantial numbers of cicadas emerged in 1975, the year *after* a dense emergence of Brood XIV in 1974. Presumably, this occurred because of malnutrition associated with extreme crowding—known from previous evidence (White and Lloyd 1975) to be a real possibility. Based on considerations (2) and (3) above, they predict that a new “Brood XV” will not become established sympatrically with Brood XIV.

There is evidence to suggest that considerations (2) and (3) above would not prevent the coexistence of broods four or more years apart. The same area in Kentucky has Brood X and XIV living sympatrically. Excavations of the nymphs (White and Lloyd 1979) show that they are living at different depths: Brood X below 15 cm, for the most part, and Brood XIV above. This is reasonable since the larger nymphs probably require larger roots and the greatest concentration of small roots is near the surface (Rogers 1940). This means, that 4-year-old nymphs may well have moved down to larger roots and would then not preempt feeding spaces from another brood lagging by as much as four years.

Based on these considerations, there is a priori reason to think that the carrying capacity of the roots of woody plants for cicada nymphs should be greater if the nymphs belong to two broods four or more years apart than if all cicadas belong to the same brood. This hypothesis was supported by the study of Simon, Karban and Lloyd (1981). This argument suggests that selection should favor 4-year jumps in the life cycle over 1-year jumps provided that the accelerating individuals are numerous enough to satiate predators.

Long Island Broods

Fig. 2 summarizes the existing information for Long Island. The patterns of stippling, cross-hatching, or discrete symbols identify the broods. Arabic numbers are keyed to place names for Brood XIV only. Locality records, dates, and sources of information are given in Appendix I. Notice that there is evidence for the presence of Brood II on Long Island (which is anticipated from its distribution on the mainland) but it occupied only the extreme western edge of the island across a narrow straight from Staten Island.

Fig. 3 attempts to place the broods of Long Island into the biogeographical context of those on the mainland. Ten broods are shown: five that occur on Long Island (XIV, X, IX, V, I) and five others (XI, VIII, VI, II, XV) that occur, or formerly occurred, nearby. Two of the broods found on Long Island (XIV, X) are also found in New Jersey, but the other three (IX, V, I) have their nearest mainland representatives 350 km or more away, in western Virginia, West Virginia, and Ohio. These, certainly, must be considered disjunct distributions.

The relevance of the other broods shown in Fig. 3 (XI, VIII, VI, II, XV)

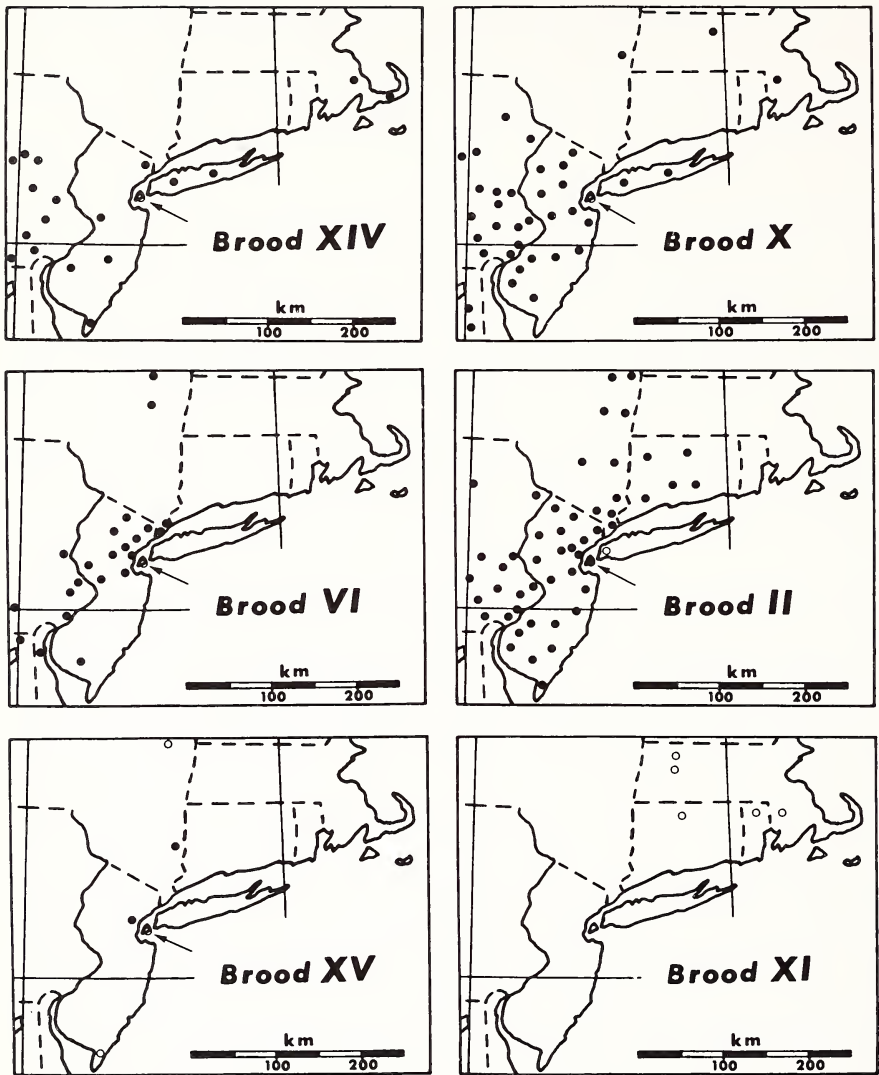
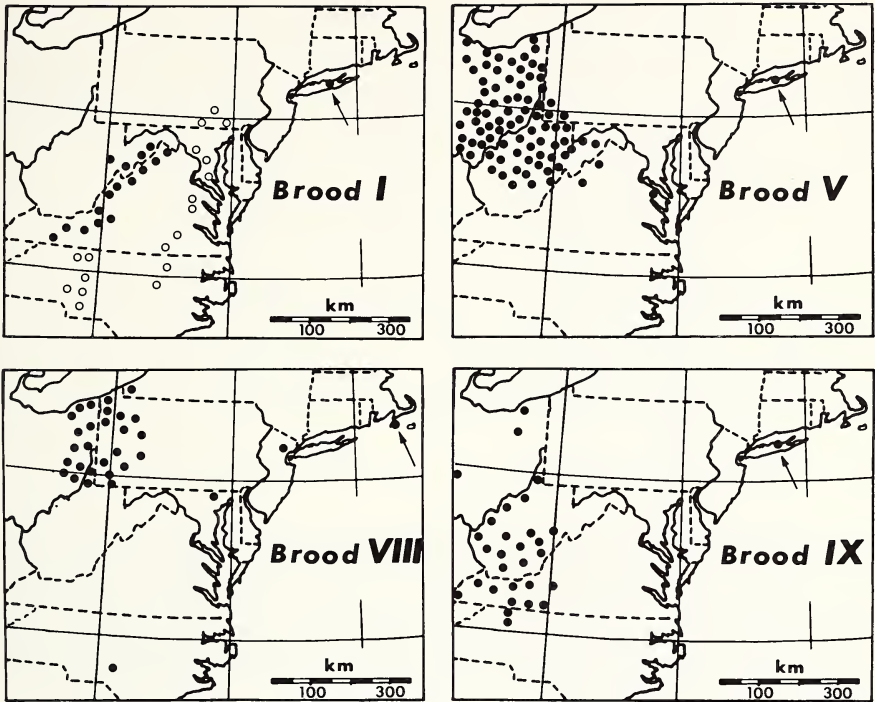


Fig. 3. Biogeography of periodical cicada broods in relation to Long Island, based on county records from Marlatt (1907). Some of these populations have subsequently become extinct; recently documented cases of local extinction are plotted as open circles rather than as solid dots. Left (above): local distributions near Long Island of the six broods on the "main sequence" of 4-year accelerations postulated by Fig. 1. All of these broods occur (or did occur) in the vicinity of Long Island (often with two or three occurring in the same county). The predominant brood on Staten Island (arrow) is II, but there are well-documented records of periodical cicadas having emerged at one time or another in synchrony with Broods XIV, X, VI, and XV (Simon 1979c). Right (facing page): complete distributions for four other broods—three of these occur on Long Island (I, V, IX) and one on Martha's Vineyard (VIII), indicated



by the arrows. These broods, according to Fig. 1, can all be derived from the “main sequence” broods by one or two 1-year accelerations, and in every case the main center of distribution of the brood is over 500 km from corresponding mainland populations.

can be judged in relation to Fig. 1. For example, Broods VI and II occur so nearby on the mainland that they may once have existed on Long Island, given rise to VI → V and II → I respectively, then later become locally extinct. On the other hand, Broods IX and X occur on Long Island (see Appendix I) so the progression may have been X → IX → V → I. The question is of unusual interest, since the two kinds of acceleration (1-year versus 4-year) are postulated to derive from very different causes.

The presence of Brood VIII on Martha’s Vineyard (Fig. 3) is interesting. In this case, IX → VIII is the only reasonable derivation we can offer, since there is no evidence that a Brood XII ever existed. The records of IX on Long Island suggest that it may also have occurred on Martha’s Vineyard at one time. Notice that the two broods on the end of the 4-year acceleration sequence, XV, and XI, are (or were) located not far from Long Island. Indeed, it can be said that the 17-year broods in southern New England and Long Island (with the exception of Brood XIV) are the most derived from the point of view of Fig. 1. Furthermore, if we allow the possibility of Brood

1- AND 4-YEAR ACCELERATION THEORY

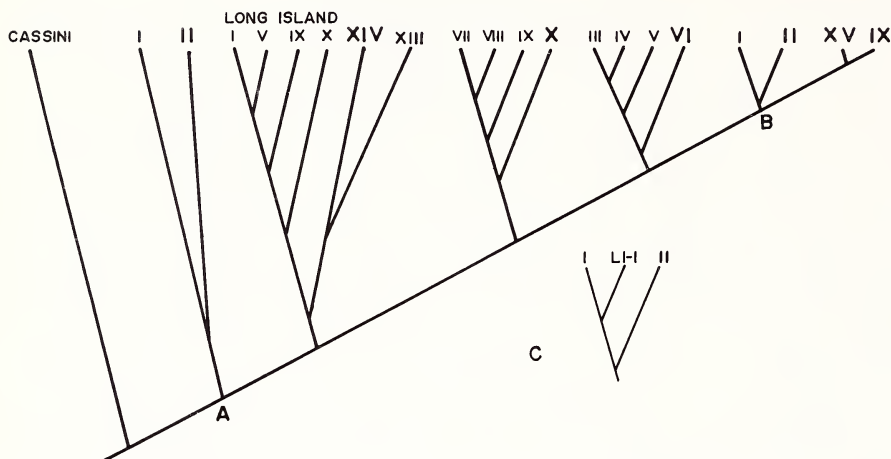


Fig. 4. A phylogenetic tree depicting the major events of Fig. 1. Large roman numerals represent broods derived via 4-year accelerations. Broods shown in parentheses in Fig. 1 are omitted from this figure. Small roman numerals represent broods formed via 1-year accelerations with the exception of the Long Island broods (see text for hypotheses of origin). "A" is the position of Broods I and II according to a separate Pleistocene refuge theory, while "B" shows the position of Broods I and II according to Fig. 1. "C" depicts Brood I plus the Long Island populations of Brood I (LI-I) as a monophyletic group.

XIV being polyphyletic, it is theoretically possible to derive the northeasternmost XIV populations from Brood XV by a 1-year acceleration as shown also in Fig. 1.

Fig. 4 summarizes, phylogenetically, the hypotheses of brood formation discussed above. Large roman numerals identify "major" broods which are largest and supposedly derived via 4-year accelerations. Smaller roman numerals identify broods derived via 1-year accelerations from larger broods. Broods I and II are shown in two positions on the tree: position "A" would result if I and II refuged separately during the Pleistocene (as suggested by Simon 1979a); position "B" would result if I and II were derived via accelerations from Brood VI (as suggested by Lloyd and Dybas, 1966). The Long Island broods are shown as derived from Brood XIV on Long Island.

Relationships of Brood XIV

Simon (1979a, b) demonstrated that both *M. septendecim* (Brood XIV) and *M. tredecim* (Brood XXIII) are allozymically homogeneous among populations sampled from a broad geographic range, but at the same time, different from each other and from conspecifics (*M. septendecim* Brood XIII, and *M. tredecim* Broods XIX and XXII). Data for thirteen populations of

Table 1. Allele Frequencies and Sample Sizes for Brood XIV, *Septendecim*.

| Locus | Allele | Allele frequency at each locality | | | | | | | | | | | | | χ^2 | |
|--------------------------------|--------------|-----------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|----------|---------|
| | | MA-A | MA-B | NY-B | NY-C | NY-D | NY-E | PA-A | MD-A | NC-A | NC-B | NC-C | KV-A | KV-B | | |
| PGM | 105 | .055 | 0 | .005 | 0 | 0 | .005 | .004 | .011 | .006 | 0 | .008 | 0 | 0 | 7.5 ns | |
| | 100 | .778 | .750 | .715 | .756 | .741 | .772 | .751 | .780 | .736 | .803 | .738 | .767 | .715 | | |
| | 98 | 0 | 0 | 0 | .005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | 95 | .217 | .250 | .280 | .239 | .258 | .222 | .239 | .209 | .258 | .197 | .254 | .233 | .284 | | 7.9 ns |
| | 90 | 0 | 0 | 0 | 0 | 0 | 0 | .005 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Sample size: α GPD-I | | 90 | 90 | 100 | 90 | 89 | 90 | 90 | 91 | 89 | 89 | 63 | 45 | 79 | | |
| | 100 | .244 | .261 | .320 | .310 | .258 | .280 | .256 | .297 | .275 | .264 | .274 | .272 | .231 | 6.6 ns | |
| | 95 | .750 | .739 | .680 | .690 | .742 | .720 | .744 | .703 | .725 | .736 | .726 | .728 | .769 | | |
| | 90 | .006 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | Sample size: | 90 | 90 | 100 | 90 | 89 | 75 | 90 | 91 | 89 | 89 | 62 | 91 | 80 | | |
| β EST | 100 | .283 | .247 | .175 | .260 | .152 | .206 | .156 | .185 | .258 | .292 | .262 | .280 | .253 | | 30.5*** |
| 95 | .717 | .753 | .825 | .740 | .848 | .794 | .844 | .815 | .752 | .709 | .738 | .714 | .741 | .741 | | |
| 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | .005 | .006 | .006 | | |
| Sample size: | 90 | 89 | 100 | 90 | 89 | 90 | 90 | 90 | 89 | 89 | 89 | 63 | 91 | 80 | | |
| MI | 105 | — | — | — | — | — | — | .078 | .061 | .044 | .054 | .033 | — | — | 3.3 ns | |
| 100 | — | — | — | — | — | — | — | .900 | .939 | .944 | .932 | .943 | — | — | | |
| 95 | — | — | — | — | — | — | — | .017 | 0 | .011 | .014 | .024 | — | — | | |
| MI | 90 | — | — | — | — | — | — | .005 | 0 | 0 | 0 | 0 | — | — | | |
| | 90 | — | — | — | — | — | — | — | — | — | — | — | — | — | | |

Table 1. Continued.

| Locus | Allele | Allele frequency at each locality | | | | | | | | | | | | χ ² | |
|-----------------------------------|--------|-----------------------------------|------|------|------|------|------|-------|------|------|------|-------|-------|----------------|---------|
| | | MA-A | MA-B | NY-B | NY-C | NY-D | NY-E | PA-A | MD-A | NC-A | NC-B | NC-C | KY-A | | KY-B |
| Sample size: PHI | — | — | — | — | — | — | — | 90 | 90 | 45 | 74 | 61 | — | — | 7.3 ns |
| | —95 | — | — | — | — | — | — | 0 | .006 | .006 | .011 | 0 | 0 | 0 | |
| | —100 | — | — | — | — | — | — | 1.000 | .994 | .994 | .989 | .991 | 1.000 | 1.000 | |
| | —105 | — | 0 | — | — | — | — | 0 | 0 | 0 | 0 | .008 | 0 | 0 | |
| Sample size: NNDH ₁ | — | 56 | — | — | — | — | — | 90 | 90 | 89 | 45 | 61 | 91 | 80 | 13.4 ns |
| | 110 | 0 | 0 | 0 | .005 | 0 | 0 | 0 | 0 | 0 | .005 | 0 | 0 | 0 | |
| | 105 | 0 | 0 | .009 | 0 | 0 | .005 | 0 | .005 | .055 | 0 | 0 | .006 | 0 | |
| | 100 | .978 | .994 | .982 | .977 | .967 | .990 | .989 | .990 | .967 | .989 | 1.000 | .977 | .994 | |
| Sample size: 95 | .022 | .006 | .009 | .017 | .033 | .005 | .005 | .011 | .005 | .028 | .006 | 0 | .017 | .006 | 13.4 ns |
| | 90 | 90 | 100 | 90 | 89 | 90 | 90 | 90 | 90 | 89 | 89 | 61 | 91 | 80 | |
| | — | — | — | — | — | — | — | — | — | — | — | — | — | — | |
| | — | — | — | — | — | — | — | — | — | — | — | — | — | — | |

Allele frequencies, sample sizes, and heterogeneity χ^2 values for Brood XIV.*

* χ^2 calculations are explained in text and have $n - 1$ degrees of freedom. ns means not significant and *** means significant at the .001 level. Localities are identified to state by the standard two letter postal code. Within states localities are as follows: MA-A, Finney Lane, Centerville; MA-B, Churchill Drive, E. Falmouth; NY-B, Janet Drive, Terryville; NY-C, Tyler Avenue, Miller Place; NY-D, Deer Park; NY-E, Applecrest Drive, Mastic; PA-A, Peters Apple Orchard on PA 94; PA-B, on I-76, 1.6 mi N. Jct. PA-23; MD-A, University of Maryland Fruit Experiment Station, Hancock; NC-A, Wacovia National Bank, Ashville; NC-B, Spruce Pine High School, Spruce Pine; NC-C, on Blue Ridge Pkwy 1.5 mi N. Jct. US 70; KY-A, on KY 70, 1 mi E. Jct. Mammoth Cave; KY-B, on US 127, 4 mi S. Swallowfield.

Brood XIV are given in Table 1 (polymorphic loci only). Twelve of the enzyme loci studied were monomorphic. Of the seven polymorphic loci, only one (β -esterase) showed any among-population heterogeneity. Workman and Niswander's (1970) formula for the heterogeneity chi-square for allele frequencies was used as a test. As a check, heterogeneity G-statistics were also calculated (Sokal and Rohlf 1969) and gave identical results. Chi-square values for each polymorphic locus are given in Table 1.

Although β -esterase varied among populations, this variation ranged from only 0.709 to 0.848 (frequency of the most common allele). Note that four of the 13 populations sampled were located on Long Island (Terryville, Miller Place, Deer Park, and Mastic; see Fig. 2 for locations). Comparing these four to the other localities, we see a larger range within a 25 mile radius on Long Island (0.740–0.848) than is found between North Carolina and Massachusetts (0.709–0.753). Furthermore, the Long Island samples were all taken from very similar pine-oak woodlands; a habitat which differs very little from that of the Massachusetts samples and which differs a great deal from the diverse montane forests of the North Carolina samples. In other words, there appears to be no consistent trend in allele frequency at the β -esterase locus with distance, latitude, or habitat type; the small amount of variation that is present appears to be random. The Long Island populations do not differ as a group from the other eight populations sampled.

Analysis of periodical cicada morphology seems to show the same picture. Examination of 48 wing-vein characters shows that populations within broods differ very little in comparison to the differentiation which has occurred among broods (Simon 1982). Discriminant analysis based on these 48 characters could not distinguish populations, but broods were clearly distinct. When the results of the discriminant function analysis were graphed, the 95 percent confidence ellipses for all Brood XIV population means overlapped almost completely. Thus we see a striking degree of morphological and allozymic homogeneity within Brood XIV and no evidence to suggest polyphyly.

Long Island Brood I

As shown in Fig. 3, Brood I occupies a large section of the Shenandoah Valley of Virginia and near-by valleys in West Virginia. In 1978, we were interested to find a population of Brood I at Ridge, New York (on Long Island) which had been described in W. T. Davis' 1927 correspondence. Several other Long Island Brood I sites were described in Davis' publications and personal notes (see Appendix I) but we were unable to confirm these. We mapped the Ridge population (Fig. 5) and also documented the presence of Brood XIV whose eggnests occurred in the exact same trees (Simon et al. 1981). We surveyed the Brood I emergence area by driving and listening

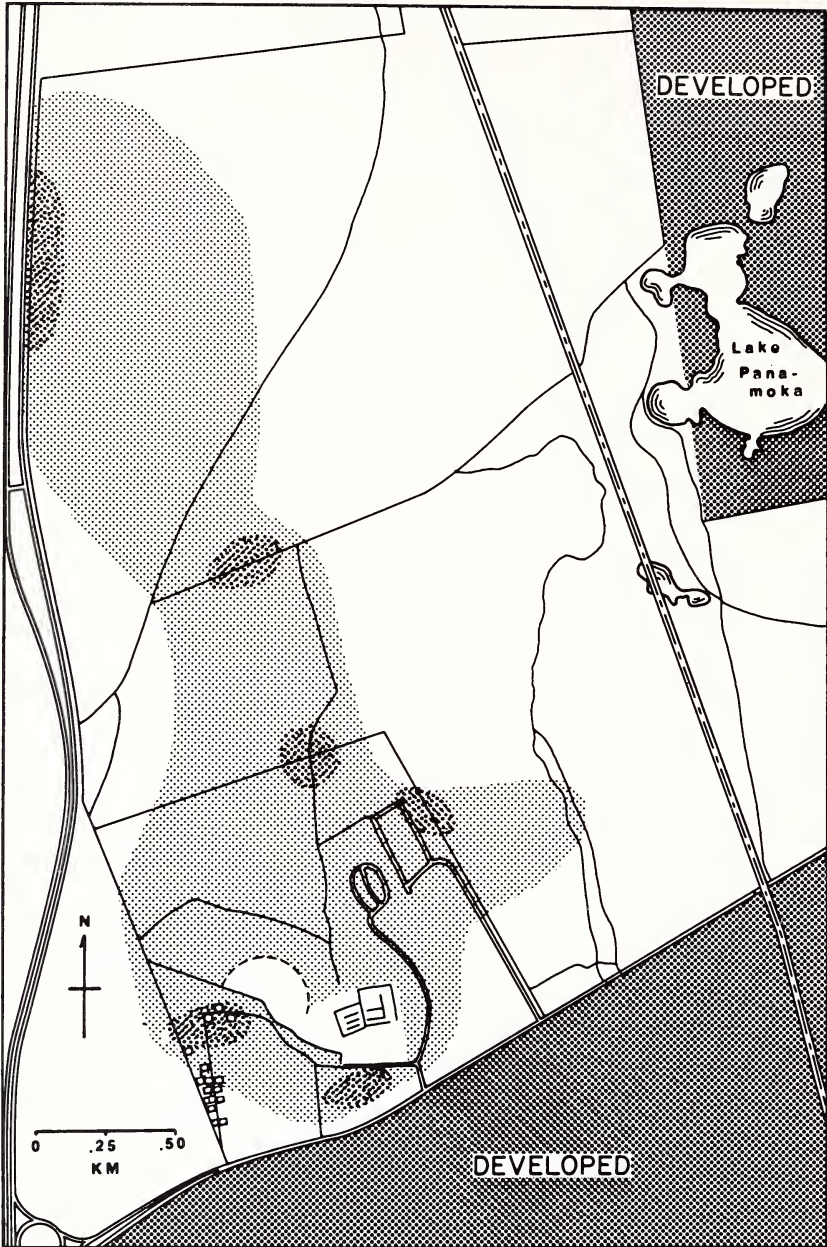


Fig. 5. Map showing the location of the study area near Ridge, Long Island. The William Floyd Parkway runs along the western edge of the map, Middle Country Road (New York Route 25) angles east-northeastward near the southern edge, and a power line runs roughly north-south just to the west of Lake Panamoka. Single lines are sandy fire lanes; double lines, paved. Areas marked "developed" are in housing; the remainder is sandy oak scrub. The oak

along the sand fire-lanes. Heavy chorusing centers of Brood I are shown in Fig. 5 by ellipses of heavier stippling among the light stippling. Broods I and XIV are the only two Long Island broods whose populations have been documented to occur in exactly the same trees. Our study site at Ridge is the only case where reproductive success of Long Island Brood I in successive generations has been verified. Notice from Fig. 2 that Brood XIV occupies a very large portion of Long Island.

The fact that Brood XIV is much more abundant in the area than is Brood I would suggest that I is derived from XIV. However, deriving I directly from XIV would be contrary to the theory (Fig. 1) which makes no provision for 4-year *decelerations*.

Given the evidence that Brood XIV on Long Island is not independently derived, the theory requires that we derive I from XIV by one of three pathways: XIV \rightarrow X \rightarrow VI \rightarrow II \rightarrow I, or XIV \rightarrow X \rightarrow VI \rightarrow V \rightarrow I, or XIV \rightarrow X \rightarrow IX \rightarrow V \rightarrow I (see Fig. 1). The third hypothesis is appealing in that there are now populations of Brood V, five or six kilometers northeast of our study site across Lake Panamoka (Fig. 2) and populations of Brood IX are known to have emerged very near there in 1918 (Appendix I; Fig. 2). Furthermore, there are a substantial number of Brood X populations on Long Island, one of which is directly south of our study site (Fig. 2). Brood VI has never been reported on Long Island and Brood II is only known from the westernmost corner of the island. In other words, the third hypothesis for the origin of Brood I is strengthened not only by the presence of the intermediary links but also by the complete absence of any other broods.

Allozymic and morphometric data.—The collection of adults from the Long Island Brood I population (LI-I) allowed us, for the first time, to examine a disjunct population, in this case separated by 275 km from the nearest recorded population of this brood and 475 km from the nearest extant population (Fig. 3). If this disjunct population was morphologically and/or allozymically distinct, we hypothesized that a phylogeny based on these data would place LI-I as the sister group of XIV rather than as the sister group of I.

A comparison of wing morphometric data (characters same as those illus-

←

scrub is almost a pure stand of *Quercus ilicifolia*, which burns at erratic intervals and is seldom more than 1.5 m tall. Interspersed are occasional pitch pines (*Pinus rigida*) and white oaks (*Quercus alba*), 3–4 m high. Blueberries (*Vaccinium* sp.) and huckleberries (*Gaylussacia* sp.) are also found, as well as sweet fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*), and winged sumac (*Rhus copallina*). Judging from eggnest scars, Brood XIV emerged throughout the oak scrub area in 1974. Light stippling indicates the area where Brood I also appeared in 1978. The heavier dots within the light stippling represent the loudest chorusing centers of Brood I. Small squares in the lower left are quadrats sampled by Simon et al. (1981).

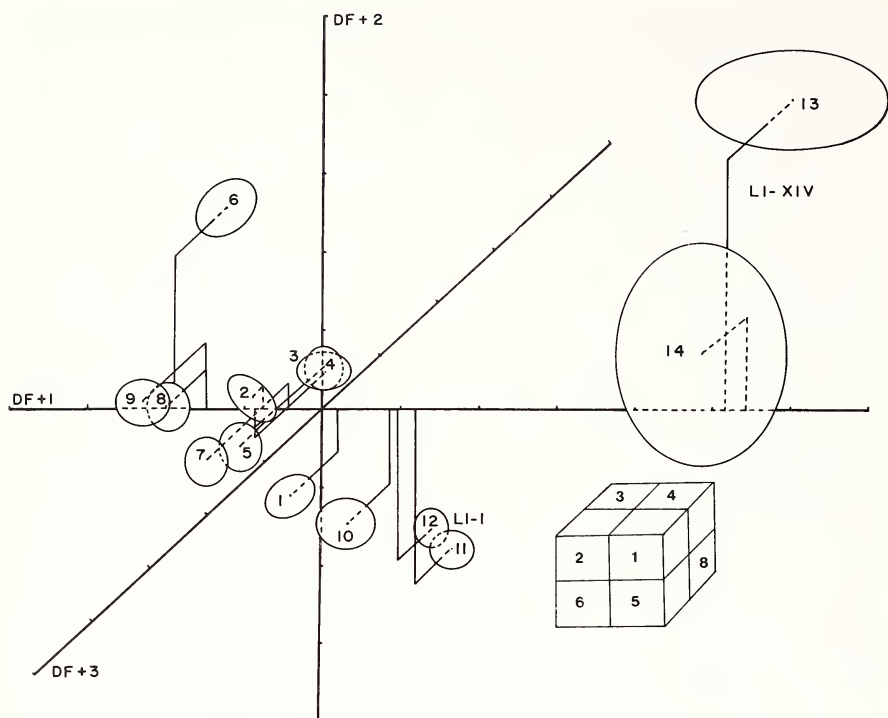


Fig. 6. Three-dimensional plot of brood mean scores of wing measurements on three discriminant function axes with 95 percent confidence ellipses about the means. Sample sizes are given in the text. If we number the octants as shown in the inset cube, then Broods I (ellipses 1-5) and II (ellipses 6-10) fall within octants 2, 3, 5, 6, and 7; LI-XIV (ellipses 13 and 14) falls within octants 1 and 4; and LI-I (ellipses 11 and 12) falls within octant 8. LI-XIV ellipses are larger due to smaller sample size per population.

trated in Simon 1982) for Broods I, II, XIV, and LI-I via discriminant function analysis is shown in Fig. 6. Sample size per population/number of populations were: 20/5, 20/5, 10/2, 20/2, respectively. Note that Broods I and II are not recognizable as two distinct groups; their populations intermingle even when plotted in three dimensions. Populations of LI-XIV and LI-I, on the other hand, are quite different from populations of Broods I and II and from each other (Fig. 6).

A phylogenetic tree was constructed using the wing morphometric data. Forty-eight wing vein characters were measured for four 17-year broods (sample size/number of populations): I (100/5), II (100/5), XIV (80/8), XIII (100/2), and LI-I (40/2); and one 13-year brood: XXIII (80/8). Five populations of *M. tredecassini* (90 individuals/5 populations) were measured to serve as an outgroup to root the tree. Many of these measurement characters were not significantly different ($P > 0.05$) among the broods examined. To

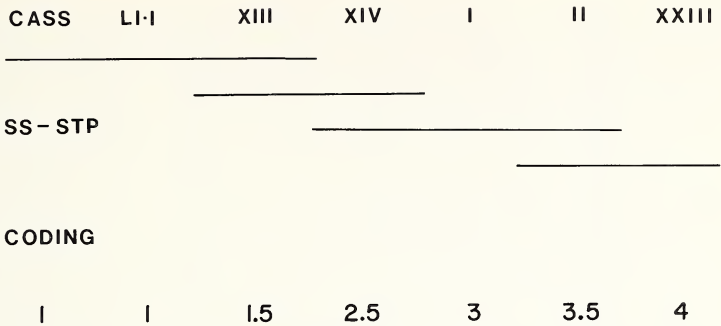


Fig. 7. An example of the coding procedure used for each of the 48 wing morphometric characters. The upper half of the figure depicts the bar diagram resulting from a sum of squares simultaneous test procedure (SS-STP) for a single character. Bars unite statistically homogeneous groups. The lower half shows the coding of the bars for that character. The coded information was used to create a phylogenetic tree using the Wagner procedure.

remove differences among populations which were not statistically significant, all broods which did not differ for a particular character were pooled. This pooling was accomplished by performing a posteriori grouping tests (sums of squares simultaneous test procedure, Sokal and Rohlf 1969) for each character and then coding the resulting bar diagrams (Simon 1983).

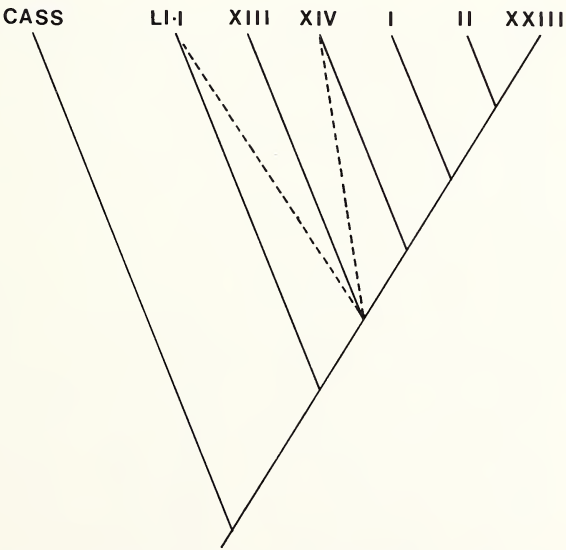


Fig. 8. Wagner phylogenetic tree based on wing vein characters. The shortest tree is represented by solid lines. Dashed lines indicate a phylogenetic hypothesis which is only 18 percent longer.

Table 2. Weighted average allele frequencies and sample sizes used in allozymic analyses. Very rare alleles are omitted from the table so that not all loci sum to 1.00. Heterogeneity chi-square (χ^2) values indicate that essentially no differentiation has occurred. Enzyme abbreviations are given in the text.

| Brood | Sample size | N | PGM | | | α -GPD | | | β -EST | | | MPI | | | PHI | | | NDHI | | |
|----------------|-------------|----|-------|-------|-------|---------------|-------|-------|--------------|--------|--------|-------|-------|-------|--------|-------|-------|-------|-------|--|
| | | | 95 | 100 | 105 | 90 | 95 | 100 | 90 | 95 | 100 | 95 | 100 | 105 | 100 | 105 | 95 | 100 | 105 | |
| XIV | 1,095 | 13 | 0.241 | 0.754 | 0.004 | 0.001 | 0.726 | 0.273 | 0.001 | 0.771 | 0.228 | 0.013 | 0.930 | 0.055 | 0.995 | 0.004 | 0.014 | 0.984 | 0.003 | |
| I | 288 | 3 | 0.221 | 0.782 | 0.007 | 0.000 | 0.752 | 0.248 | 0.000 | 0.844 | 0.156 | 0.003 | 0.966 | 0.031 | 1.00 | 0.000 | 0.009 | 0.983 | 0.008 | |
| II | 384 | 6 | 0.254 | 0.740 | 0.006 | 0.000 | 0.717 | 0.283 | 0.000 | 0.821 | 0.179 | 0.010 | 0.961 | 0.029 | 1.00 | 0.000 | 0.010 | 0.981 | 0.010 | |
| LI-I | 96 | 1 | 0.203 | 0.792 | 0.005 | 0.000 | 0.708 | 0.292 | 0.000 | 0.812 | 0.188 | 0.021 | 0.969 | 0.010 | 0.964 | 0.036 | 0.000 | 0.985 | 0.010 | |
| χ^2_{3df} | | | 3.4* | 4.6* | | | 2.6* | 2.5* | | 19.7** | 19.1** | | 19.9† | 18.1† | 45.6†† | | | 0.4* | 6.6* | |

* Not significantly heterogeneous.

** Significantly heterogeneous at the 0.001 level but I, II, and LI-I are not significantly heterogeneous and LI-I and XIV are not significantly heterogeneous.

† Significantly heterogeneous at the 0.001 level but I, II, and LI-I are not significantly heterogeneous and XIV and II are not significantly heterogeneous.

†† Significantly heterogeneous at the 0.001 level but I, II, and XIV are not significantly heterogeneous.

An example of the coding procedure is given in Fig. 7. This procedure retains more information than previously proposed coding procedures (Mickey and Johnson 1976). The coded data was used to construct a phylogenetic tree using the Wagner-78 program written by J. S. Farris (see Farris 1970). The resulting tree is shown in Fig. 8.

The phylogenetic tree based on wing morphometric data places the LI-I populations in the most ancestral part of the tree. Because it is so unlikely that the small population of Brood I on Long Island could be a remnant of the ancestor of Brood XIV, which covers much of the eastern United States, alternative phylogenetic hypotheses were examined. Alternative trees which placed LI-I as the sister group of I and II or XIV were examined but proved to be less compatible with the data (i.e., produced much longer trees). It was, however, possible to create a tree in which Broods XIV, XIII, and LI-I all originated at approximately the same time. This tree (shown by dotted lines in Fig. 8) was only 18 percent longer than the shortest tree. No significance tests exist for comparison of phylogenetic trees.

The morphometric phylogenetic hypothesis generated above could be explained by the following evolutionary scenario. Brood XIV was the ancestral brood and at one time covered most of the eastern United States. Very early in its history it gave rise to Broods XIII and LI-I. Broods I and II were later derivatives followed by the conversion of southern populations into 13-year Brood XXIII. This scenario is compatible with Lloyd and Dybas' (1966) scheme shown in Fig. 1.

Allozymic analyses of Broods I, II, LI-I, and XIV were less informative. Table 2 presents the results. Heterogeneity chi-square values indicate that essentially no differentiation has occurred. The enzymes α -glycerolphosphate dehydrogenase (α -GPD), phosphoglucumutase (PGM), and nothing dehydrogenase (NDHt) are homogeneous in allele frequency across all broods. Esterase (β -esterase) shows significant differentiation but Broods I, II, and LI-I taken as a group are not significantly heterogeneous and LI-I and XIV taken as a group are not significantly heterogeneous. Mannosephosphate isomerase (PHI) is significantly heterogeneous across all broods but I, II, and LI-I and XIV and II are not significantly heterogeneous. Phosphoglucose isomerase (PGI) is significantly heterogeneous across all broods but I, II and XIV are not significantly different as a group. In other words there is little allozymic information on which to base a phylogenetic tree.

Clearly, additional data are needed. Populations of LI-V will be collected in 1982 in addition to Brood V from Ohio, West Virginia and Virginia. These cicadas will be analyzed both allozymically and morphometrically. We can say, however, that LI-I is morphologically different from Broods I, II and XIV and that a phylogenetic analysis suggests that LI-I evolved independently of Brood I in Virginia.

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Appendix I

This appendix summarizes Long Island periodical cicada locality records. This compilation is useful as many of the records are not conveniently accessible being contained in newspapers, private notes, and old, not widely circulated journals. Localities are organized by brood in chronological order.

Brood I.—1910: “. . . in the Half Way Hollows near Wyandanch, Long Island” at the Holmes farm, “they had been very numerous The species occurred in great numbers in the same territory [same trees] in 1906

In the Long Island locality [in 1910] they were certainly numerous enough to lay a great many eggs, and may possibly establish a new brood" (Davis 1910). "It was ascertained, however, that the cicadas had occurred in great numbers in still another locality in 1910, in a place further to the north [of the Holmes farm] and nearer to the Dix Hills" (Davis 1911). **1927:** In a letter to W. T. Davis from Albert A. Arnold dated July 11, 1927, Arnold reports *Magicicada* at two localities: 1) Along Middle Island Road (from Coram) near Camp Upton (now Brookhaven National Laboratory) "covering all the scrub oaks"; 2) On the road leading from Coram to Riverhead on the flat portion of land just east of "the road which formerly led into Camp Upton property and extending for quite some distance on both sides of this road." A reference in W. T. Davis' personal notes explains that *Magicicada* collected from Camp Upton on June 15, 1927 were "found in abundance." **1944:** In a letter to W. T. Davis dated June 22, 1944, Roy Latham listed the following periodical cicada localities: 1) Dix Hills in between Commack Road and Deer Park Avenue south of 25; 2) on 25 several miles east of Ridge, on the north side of the road, "a small colony"; 3) on 25 near the junction of 25A (east of Ridge) and for a mile farther. "Just east of there" he reports "a large colony on both sides of the road—greatest abundance on the north"; 4) Along old country road, north of Riverhead and on 25. Scattered individuals were seen "up to two miles east of Riverhead."

Brood II.—1911: "The 17-year cicada occurs on Long Island, New York, in numbers at the most unexpected times Brood 2 [1911] was in its usual abundance on Staten Island and in the valley of the Hudson, but on Long Island very few of the cicadas were found But one or two individuals were reported from the western end of the island during 1911" (Davis 1915). **1945:** We have found no reference to Brood II in 1945 other than this strange article from *Newsday*, May 30, 1974—"Everyone remembers Brood II, which covered Long Island in 1945 and left newspaper editors, pesticide manufacturers and other disaster-lovers counting the years until it was due again in 1962. Only, Brood II did not keep its appointment." **1962:** On June 14, 1962, *The New York Times* published a small article entitled, "Scientists Mystified as 17-year Locust Shuns Two Counties." In this article they commented on the extreme abundance of cicadas in the Hudson Valley, metropolitan New Jersey and Staten Island and added, "but in Westchester and Nassau counties, the schedule notwithstanding, the shrill cry of the locust has not been heard."

Brood V.—1914: Davis (1915) wrote, "Returning to Wading River on July 24 [1914], we noticed from the car window, about a mile to the west of the railroad station, many oaks and other trees on the north side of the track in which the cicadas had laid their eggs, causing the death of the smaller branches . . . we found that the seventeen-year cicada had been very common about Deep Pond and on the easterly side of Long Pond [now Lake Panamoka]

. . . Under the date of June 9, 1914, Dr. Frank Overton . . . wrote me that the seventeen-year cicadas were spread over several square miles northwest of Calverton, about two miles from the Deep Pond locality mentioned above. He said that he had taken particular notice of them for three miles along the Riverhead, Coram road about one or two miles north of the station. They reached all the way to the elevated lots and even scattering ones were found nearly into Riverhead." Davis (1924) presumably reasoning from 1914 records predicted that, Brood V would appear "in 1931 in the Half Way Hollow Hills, also in the hills north of Holbrook and at Wading River." **1965:** On June 6, 1965 *The New York Times* noted that, ". . . 17-year locusts were reported this week in the Lake Panamoka area of Wading River and a vast peach orchard off North Road in Calverton." *Newsday* also carried the story: ". . . the insects have appeared this year on Long Island in Calverton and around Lake Panamoka near the Riverhead-Brookhaven town line." Brewster (1965) reported that ". . . May 23rd the 17-year locust (periodical cicada) emerged in wooded areas at Lake Panamoka and several days later at Calverton." A population of cicadas was noted at the Transient Camp Area of Wildwood State Park, Wading River and also across from the picnic and parking areas (J. R. Wildt pers. comm.). They were also seen along River Road in Calverton, in Lewin's Peach Orchard adjoining Wildwood State Park (R. H. Brewster pers. comm.), and on 25A approximately one mile southeast of the junction of Sound Avenue (John Waskewicz pers. comm.) in that same year (1965). In 1982 they were again seen in Wildwood State Park (Camping area E and adjoining Lewin's Orchard). They were very abundant east of the junction of 25A and 25. Oviposition was relatively heavy along the roadside but no flagging was observed.

Brood IX.—1918: Davis (1920) found periodical cicadas "in the woods along the road between Manorville and Wading River." He collected some "about one mile north of the Middle Country Road." These were the only ones observed in 1918 and none were there in 1919.

Brood X.—1902: Davis (1920) quoted the eighteenth report of the N.Y. State entomologist (1902, p. 113) as follows, "The insects were observed . . . at Wantagh, Nassau Co., also between Massapequa and Amityville, between Sayville and Oakdale, east of Patchogue to Brookhaven and also to the north of Medford and Holtsville, and a small brood [sic] northeast of Riverhead, all in Suffolk Co." Davis (1907) reported that although a friend had seen hundreds of exuviae of the 17-year locust in Prospect Park, Brooklyn, he had only obtained three adults and he "attributed their scarcity to the English Sparrow." **1919:** *The New York Times* of June 17th 1919 (p. 25: 3) talked with farmers in the vicinity of Farmingdale, Bethpage, and Massapequa who reported thousands of cicadas doing damage to fruit trees and other hardwoods. Old residents claimed that 17 years before they were not nearly so numerous. Davis (1919) recorded "17-year cicadas singing at Mas-

tic, L.I. during the first week of June." In another publication (Davis 1920) he noted them as occurring on South Country Road just east of Carman's River, and in the woods just east of Patchogue; also from Wantagh to Farmingdale and as far north as Central Park on Long Island; finally, north and east of Massapequa rail road station. **1936:** *The New York Times* (June 12, 1936, p. 4:7) reported that the cicadas were found "first in Carmen Ave., Farmingdale . . . since then the swarms have been reported at Massapequa, and all through Suffolk scrub oak along the Motor Parkway from Medford westward to Farmingdale." They were also seen along the Sunrise Highway in Massapequa Park. **1970:** *Newsday* (June 5, 1970, p. 12) lists two exact localities Skylark Drive (Holtsville) and Springdale Drive (Ronkonkoma). They explained that "officials of the State Conservation Department and County Agricultural Extension Service said . . . that they have received hundreds of complaints this month about the insects. Most of the calls have come from an area including Ronkonkoma, Holtsville, Islip, and Sayville, where the influx is concentrated." The same newspaper (June 23, 1970) reported 17-year cicadas in Bohemia on eighth Street near the South Side Sportsman's preserve. They must have been abundant because, "50 Bohemia residents . . . signed petitions appealing for help to fight the alarming problem of swarming cicada locusts [sic]."

Brood XIV.—**1906:** From personal observation and from other sources, Davis (1923) discovered that the 1906 Brood XIV covered "in a general way territory along the north shore from Oyster Bay to Wading River, extending south to Farmingdale and eastward through the central portion of the island to Manorville. There were also colonies at Moriches and Eastport." Davis (1907) additionally noted that cicadas were collected in Yaphank in 1906 from the same locality in which they were exceedingly abundant in 1855. **1923:** Davis (1924) reported that "during the summer [of 1923] I received . . . considerable information regarding the distribution of [Brood XIV] The area already given for the appearance of the brood in 1906 was almost exactly duplicated." In the same paper, Davis mentions finding two species (*M. septendecim* and *M. septendecula* from the descriptions) at the Holmes farm near Wyandanch. "The large form extended southward to the railroad and beyond." This locality is important because Davis reported finding Brood I in the same apple trees in 1910 and 1944. *The Brooklyn Eagle* (June 5 and 6, 1923) noted that cicadas were heard in Yaphank and Camp Upton on the previous Saturday. Among Davis' personal notes and letters, we found the following exact locality descriptions: 1) May 30, 1923 F. M. Schott saw many cicada openings in the ground and later heard them in Pinelawn and Wyandanch; 2) Arthur H. Helme saw cicadas "in great numbers 1 mile east of Port Jefferson between Port Jefferson and Crystal Brook at the place known as Old Place (letter of June 6). On June 14 (in

litt.) they were still emerging at Belle Terre and there was a colony at Middle Island. Helme also noted great numbers of these insects from a point south-east of Port Jefferson Station all along the route from there to Rocky Point, along the wooded stretches south of the new state road, and at some spots extending north of the railroad; 3) Edward Bell (letter of June 18, 1923) said that the cicadas were continuous along the Motor Parkway from Farmingdale to the road running from Smithtown to Islip; 4) J. Nichols (letter of June 20, 1923) reported seeing the cicadas in the woods boarding the Mastic railroad station; 5) Roy Lantham (letter of August 24, 1923) searched the island from Orient to Calverton and never found them east of Calverton; 6) Finally, E. S. Miller (letter of September 12, 1923) summarized, "they seemed to work in a strip across the island from Rocky Point to South Setauket in width and thence across the island through Ridge, Middle Island and Coram, thence across to the south side—Moriches to Brookhaven (worst from Ridge to Coram). 1957: *The New York Times* (May 28, 1957) notes "the heaviest infestation is reported in the Huntington-Deerpark area. None has been reported in Nassau County." 1974: *Newsday* (May 30, 1974) listed two street addresses (52 Livingston St., Deer Park; 171 Eastwood Ave., Deer Park) and said that county agents received approximately 350 calls from "an area ranging from Hicksville in the west to Mastic and Port Jefferson in the east, with a concentration from the Medford and Dix Hills-Deer Park area." *Newsday* (May 31, 1974) reported cicadas at 19 Deer Lane, East Setauket. The following list of localities was compiled in 1974 (1 = personal observation, 2 = record of county agent, 3 = record of exterminators): Babylon (3), Belle Terre (1), Bohemia (2, 3), Brentwood (3), Brookhaven Labs (1, 2), Calverton (3), Center Moriches (2), Coram (1, 2), South Commack (1, 3), Deer Park (1, 2), Dix Hills (1, 2), East Setauket (1, 2, 3), Farmingville (2), Hicksville (2, 3), Manorville (2), Massapequa (3), Mastic (1, 2), Medford (3), Middle Island (3), Miller Place (1), Patchogue (2, 3), Port Jefferson Station (1, 2), Ridge (1, 3), Riverhead (2), Rocky Point (3), Ronkonkoma (2), Shirley (3), Sound Beach (2), and Terryville (1, 2).

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